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Point-of-view

Rethinking classic starling displacement experiments: evidence for innate or for learned migratory directions?

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In an attempt to encourage the discourse on sources of individual variation in seasonal migration patterns and the microevolution of bird migration, we here critically examine the published interpretations of a now classic displacement study with starlings *Sturnus vulgaris*. Based on the ring recoveries after experimental displacement towards the south and southeast of Dutch capture sites of over 18 000 hatch-year and older starlings, in a series of analyses published in *Ardea* from 1958 to 1983, A. C. Perdeck established that displaced starlings showed appropriately changed orientations only when they were experienced. During both southward and northward migration, released adults navigated to an apparently previously learned goal (i.e. the wintering or the breeding area) by showing appropriately changed orientations. Juveniles showed appropriate directions when returning to the breeding grounds. In contrast, during their first southward migration displaced juveniles carried on in the direction (and possibly the distance) expected for their release at the Dutch capture site. From the mid-1970s this work has become cited as evidence for starlings demonstrating 'innate' migratory directions. If the definition of innateness is 'not learned by the individual itself', then there is a range of non-innate influences on development that are not ruled out by Perdeck's experimental outcomes. For example, young starlings might have carried on in the direction that they learned to migrate before being caught, e.g. by observing the migratory directions of experienced conspecifics. We argue that, despite over 60 citations to Perdeck as demonstrating innate migratory directions, the jury is out.

Keywords: innate, learning, migration, navigation, ontogeny, orientation

Introduction

The extent to which phenotypic traits are shaped by genetic information directly and uniformly, or directly yet following environmentally shaping via 'reaction norms', or fully moulded during individual development in interaction with the environment by processes of phenotypic plasticity and learning, remain at the heart the main contemporary evolutionary debate (West-Eberhard 2003, Gilbert and Epel 2009, Jablonka and Lamb 2014, Laland et al. 2014, Wray et al. 2014). Answers to these questions will also illuminate the sources of individual variation in seasonal migration patterns (e.g. genetic variation or different experiences during early development; van Noordwijk et al. 2006, Harrison et al. 2010, Verhoeven et al. 2019), and indeed the microevolution of bird migration (Alerstam et al. 2003, Pulido and Berthold 2010, Piersma 2011, Gill et al. 2019, Winger et al. 2019). In this dialogue, at least with respect to bird migration, studies on displacement experiments with young and older birds of a species have played a central role. To open-up and encourage this evolutionary discussion, and to emphasize the contributions of studies on migratory birds, in this Point-of-view we aim to 'rethink' the published interpretations of these early experimental studies of bird migration.

Starling displacement experiments

In five papers published between 1958 and 1983 in the Dutch ornithological journal 'Ardea', Albert C. Perdeck, aiming to study orientation mechanisms, presented and discussed the results of three massive displacement experiments with starlings *Sturnus vulgaris*. 1) In the months of October and November 1948–1957, totals of 7460 juvenile (hatch-year) and 3787 adult starlings were captured during migration in the dunes of the province of Zuid-Holland, the Netherlands, flown to one of three airports in Switzerland (Basle, Zürich or Geneva) and released, usually within 24 h after capture (but see details in Perdeck 1958). 2) In October and November 1959–1962, totals of 2703 juvenile and 885 adult starlings were captured, again in the dunes of southwest Netherlands, and flown to Barcelona, Spain, for immediate release (Perdeck 1964, 1967). 3) In February and March 1964–1971, about 3400 juvenile starlings captured in 'the middle of the Netherlands', were transported to and immediately released in either Zürich in Switzerland or nearby Radolfzell in Germany (Perdeck 1974, 1983). These releases subsequently yielded several 100s of recoveries. Comparisons of the locations between groups that were differently displaced and those of non-displaced starlings captured in the Dutch dunes, formed the basis of Perdeck's inferences.

This experimental displacement of more than 18 000 starlings over a period of 24 years came after a flurry of similar but smaller displacements, often to study 'homing', in several bird species in Germany in the 1930s; many of the results were published only after the 2nd World War (Krätzig and Schüz 1936, Rüppell 1937, 1944, van Oordt 1943, Rüppell and Schüz 1948, Schüz 1949, 1950a, b). This German work inspired comparable efforts in North America (Griffin 1940, Rowan 1946). In the Netherlands, Perdeck's experiments with starlings must have gestated during the pre-War years in the intellectually stimulating setting of 'Vogeltrekstation Texel', involving luminaries such as L. Tinbergen, H. Klomp and H. N. Kluyver. In fact, as a try-out, already in 1938 some 600 starlings were captured in the Netherlands and transported before release at Avranches, Lower Normandy, in northwest France. 'The outbreak of the war made an end to this experiment before results were obtained' (Perdeck 1958).

The three displacement experiments represent successive steps in an examination of ontogenetic aspects of orientation, as a component of navigation, in migrating birds. To introduce the first experiment, Perdeck (1958) showed a clear scheme on how recoveries after displacement of actively migrating birds moving in a supposed 'preferred direction', would demonstrate either 'one-direction orientation' (later called 'vector navigation' by Able 2000), or 'true goal orientation' (Kramer 1952; Fig. 1). The release of naïve juveniles and experienced adults showed unambiguously that, upon release after a displacement of ca 600 km towards the SSE, juveniles continued in directions quite similar to the ones released at the catching location (i.e. showing one-directional orientation), whereas adults showed reorientation towards the NW to end up in the normal wintering area (i.e. showing true goal orientation; Fig. 1). Juveniles that were released jointly with the adults were recovered at the same general locations as juveniles that were released separately. Likewise, adults released jointly with the juveniles ended up in the same locations as the separately released adults. The second experiment, with displacements to Barcelona, northeast Spain, confirmed the previous results (Perdeck 1967), although a comparison with the Swiss releases suggested that, depending on the time of release and the suitability of the release area, juveniles either continued in the preferred 'Dutch' direction or, especially if released later in the year, halted to winter locally (Perdeck 1964). This work lead to the third, late winter, displacement experiment, which demonstrated that birds in their first winter were in fact capable of true goal orientation on their first return migration to the breeding areas, just as adults (Perdeck 1974, 1983).

This body of work has become a 'classic'. The maps from Perdeck (1958) have been used to illustrate goal orientation by adult starlings in at least 12 textbooks on bird migration (Drost 1962, Matthews 1968, Schüz et al. 1971, Baker 1978, Mead 1983, Alerstam 1990, Burton 1992, Berthold 1993, 1996, 2001, Newton 2008, 2010; Fig. 1). In an even-handed early review of orientation and navigation, Emlen (1975) spent five pages reanalysing and considering Perdeck's experiments. And by now, according to the Web of Science, the paper has been cited over 200 times. Although the direct, factual representations of Perdeck's findings usually are accurate, we suggest that there are issues with the interpretations in several of the citing books and in many of the journal publications referring to Perdeck (1958). Although part of the publications rightly refer to Perdeck's experiments as evidence for learning, many publications refer to Perdeck as evidence that young starlings follow an innate compass direction. We take issue with this interpretation.

The history of 'innate' interpretations

Although the term 'innate' can have several different meanings in biology, which nevertheless are rarely made explicit

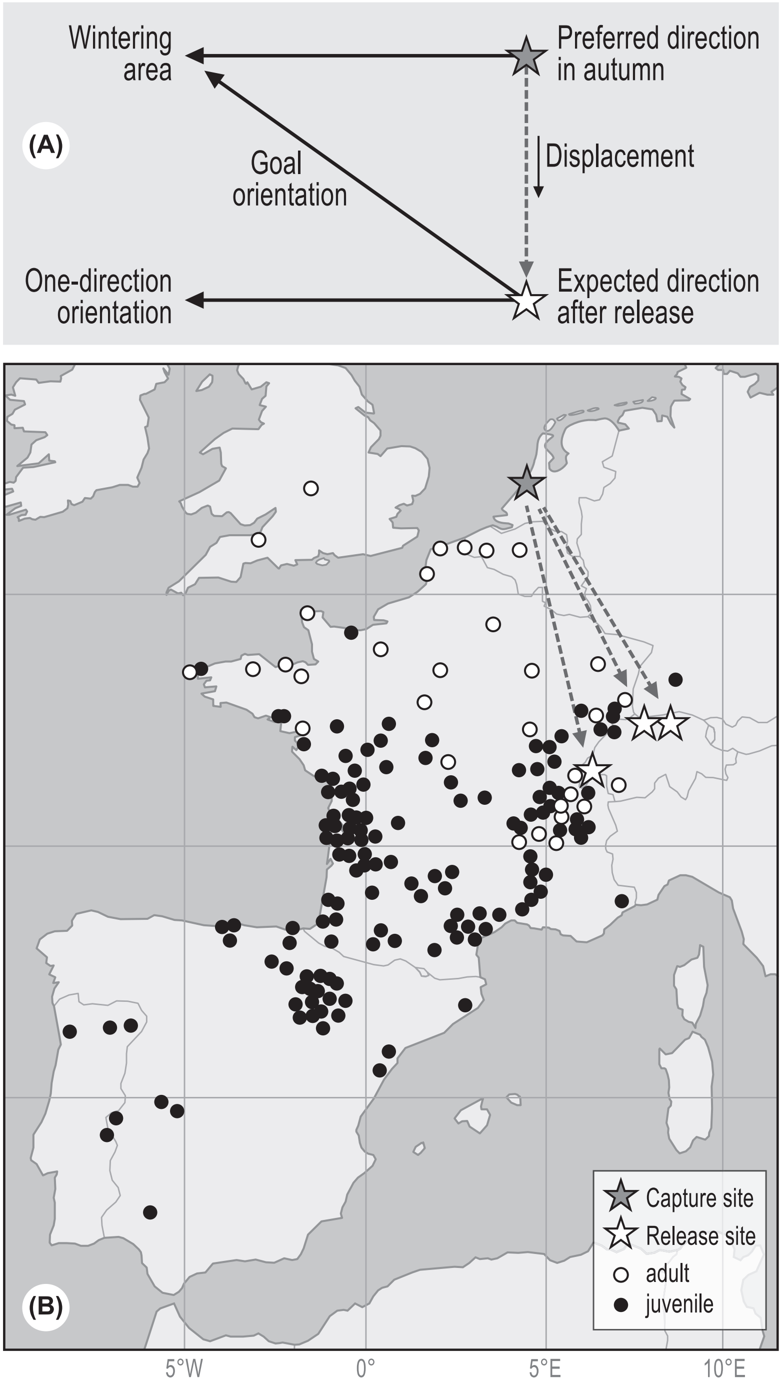

Figure 1. A visual of the orientation hypothesis tested by Perdeck (1958) in his displacement experiments with starlings (top panel) and the distribution of the recoveries from 3 release points in Switzerland of adults (open circles) and juveniles (closed dots) during the ensuing autumns and winters (lower panel). Both panels are based on Perdeck (1958), but this version is modified from Newton (2008).

(Bateson 2000, Mameli and Bateson 2011), we think that in the context of the migration studies the meaning of innate behaviour usually is: behaviour that is not learned by the individual itself. Perdeck himself had been extremely careful in his interpretations of the contrasting findings for juvenile and adult starlings. Following Geyr von Schweppenburg (1933), Perdeck realized that the term 'innate' is ambiguous, and proposed to call the specific direction in which young birds fly without contact with adults their 'preferred direction', a term with no further connotations as to the other factors that might have influenced its development. However, as we will see below, since the mid-1970s it has become commonplace to use Perdeck (1958) in direct support of statements like 'inexperienced juveniles followed an innate clock and compass strategy (e.g. vector navigation), leaving at the right time and flying the correct distance in the inherited migratory direction' (to quote a recent review, underlining is ours, by Merlin and Liedvogel 2019). We actually have made such citations ourselves (Ens et al. 1990, Verhoeven et al. 2019). In many cases the attribution is more implicit, with other references being cited too. A recent case is: 'simple, compass-based, vector orientation relying on an inherited initial direction seems to be the only mechanism available to many inexperienced animals that travel without experienced companions' (Mouritsen 2018).

Analysis of references to Perdeck (1958)

To elaborate the claim that the ambiguity with respect to Perdeck's results showing evidence for learning or rather for a 'behaviour that is not learned' ('innate'), we quantified how Perdeck's work has been interpreted. We first reviewed 12 books summarizing the contemporary state of knowledge on bird migration and assembled the ways in which Perdeck (1958) was cited (reproduced as Supplementary material Appendix 1). In August 2019 we used the Web of Science to search for journal articles citing Perdeck (1958) in relevant ways. We had to do this 'indirectly' (through one of the papers in WoS citing Perdeck 1958), as a direct search would not yield the 1958 paper. We found that 89 papers were relevant and digitally available, so that we could search the downloaded pdf's for the text accompanying the citation of Perdeck (1958). Of the 89 papers, 36 were reviews and the rest were topical articles. All the pertinent citations were assembled in a table, which is reproduced as Supplementary material Appendix 2.

For each book or journal article we scored the way in which the findings of Perdeck (1958) had been interpreted. We distinguished three different interpretations. The first was in line with Perdeck's own, allowing the option that the juvenile starlings maintaining the migratory direction of their capture location after displacement reflected learning. This is opposed to newer interpretations of Perdeck's findings as evidence for 'innate', 'inherited' or 'programmed' orientation behaviour, or a combination of these and/or similar terms (Supplementary material Appendix 2). Such attributions could either be 'indirect' (i.e. the Perdeck results being implicated in statements based on other studies), or direct. We acknowledge that there is an element of subjectivity in these assessments, which is why we reproduce all quotes in the Supplementary material Appendix 1–2, with specific indications of the exact formulations that made us assign citations to one of the three categories.

The three books published between 1962 and 1971 very factually reported Perdeck's findings. However, starting with Baker (1978), eight of the nine textbooks discussing Perdeck (1958), attributed the possibility of birds showing innate migratory directions to the outcomes of his experiments (Supplementary material Appendix 1). At the same time, from the mid-1970s onwards, the finding that displaced young starlings (but not adults) continued in the direction expected from their place of capture, also in the journal articles became cited as having established the existence of innate directions (Supplementary material Appendix 2). Of all 89 publications, 53 (60%) refer to Perdeck (1958) as providing evidence for 'innate' orientation behaviour. In 30 of 53 cases (56%) this interpretation was attributed directly to Perdeck (1958); in the remaining 23 cases the attribution was indirect, invoking other studies to support notions such as 'endogenous vector programmes' (Wehner 1998) or 'genetically encoded programmes' (Muheim et al. 2018).

We suggest that these new attributions reflected the increasing popularity of the neo-Darwinian mind-set (Mayr 1952, 1961, Laland et al. 2011). The interpretation was enforced by 1) the impressive differences between closely related species of *Sylvia* warblers in the amount and timing of migratory restlessness (correlated with natural migration distances) of juveniles raised in isolation from the egg phase (Berthold 1973), and 2) the spontaneous temporal changes in the escape directions in octagonal registration cages of hand-raised garden warblers *Sylvia borin* (Gwinner and Wiltschko 1978). A typical quote from this time is by Wiltschko and Wiltschko (1978): 'The large scale displacement experiments of Perdeck (1958, 1967) clearly demonstrated that young birds on their first migration did not compensate for the displacement and thus apparently do not fly towards a goal, but on a standard direction. Many hand-raised birds isolated from adults showed in cages directional tendencies coinciding closely with the migratory directions of their free-living conspecifics, … indicating that the information of the migratory direction is indeed innate.' Even though the experiments with hand-raised songbirds suggest that migratory direction may have a strong 'innate' component in the sense that it is not learned by following others, we argue that Perdeck's experiments did not demonstrate this.

Why Perdeck did not show 'innate' orientation?

As noted by Matthews (1968, p. 10): 'Where young and old migrate together the former could possibly learn the migration direction as well as the final location of the wintering area.' Indeed, although both Thorup et al. (2007) and Rabøl (1978) have cited Perdeck (1958) as showing evidence for innate migratory directions (Supplementary material Appendix 2), in a joint publication they state the opposite: 'the starling is a highly social, diurnal, short-distance migrant. This means that (Perdeck's) result could be influenced by social interactions' (Thorup and Rabøl 2007). For this reason, we join Matthews (1968, p. 15) in concluding that 'it is therefore regrettable that the results (of the displacement experiments) cannot be taken as conclusive proof of the existence of an innate directional tendency in the experimental birds.' The hatch-year starlings captured by Perdeck's teams in the dunes near the Hague no doubt had been migrating for some time themselves and were likely part of migrating flocks. These flocks will have been composites of more or less experienced individuals. Thus, the young birds could already have learned, by non-social or social means, the direction they were supposed to fly in at the moment that they were transported to Switzerland.

In this light it is noteworthy that the direction taken by juveniles displaced to Switzerland was approximately 20-degrees more southward than the direction observed in the Netherlands. Perdeck (1958) offered four explanations for this discrepancy: 1) different methodologies, 2) different years of study, 3) different topographies (called 'leading lines' by Perdeck) and, perhaps most interestingly, 4) different flock compositions. The last point refers to the possibility that the direction observed in the Netherlands is actually a compromise between the true goal navigation of adults and the preferred direction of juveniles. If so, the 20-degree deviation from expectation observed after displacement might show us the uncompromised preferred direction of juveniles.

We believe that Perdeck was correct in considering the possibility that the observed direction in the Netherlands was a compromise between different 'kinds' of individuals, but why did he not offer the same explanation for the direction taken by juveniles after displacement? As an alternative to the later interpretations, i.e. that the displaced juvenile starlings demonstrated the use of 'innate', 'inherited' or 'genetic' information on migratory directions, the experimental birds could simply have demonstrated that they (partly) learned their migratory directions from 1) asocial learning before displacement (e.g. through the reward of food, safety and/or warmth when flying over land instead of water; see discussion by Kendal et al. 2005), 2) the guidance by, or imitation of, experienced adults before displacement, 3) asocial learning after displacement (e.g. in dealing with 'leading lines' in Switzerland) and 4) social learning from local adults after displacement to Switzerland.

The present state of the art

We will round off by presenting a tantalizing example of the complexities of early development of migratory direction in a social bird species. It begins with the results obtained from the pre-War westward displacements of hand-raised white storks *Ciconia ciconia* across their European migratory divide from what was then Rossitten in east Prussia (Schüz 1949, 1950a, b, Mayr 1952, and see Schüz 1938 for an impression of the flavour of the place and the research effort). Hand-raised eastern white storks transported towards the west, and released after the local (western) storks had departed south, showed significantly more easterly bearings (Schüz 1949) than the 'controls' released earlier. The early released birds clearly migrated in the company of locals in south-westward directions (Schüz 1950a). Note, however, that the late-released displaced eastern birds were not quite as south-easterly oriented as expected (Wallraff 1977). Repeated late-release experiments with naïve eastern storks in Latvia (Katz 1986, cited in Chernetsov et al. 2004) yielded southwesterly, rather than the expected southeasterly, migratory directions.

In an effort to settle the matter, Chernetsov et al. (2004) again hand-raised eastern white storks in what was then the Rossitten and is now the Rybachy area. This time the storks were displaced eastward and released at either normal departure times or after the departure of local birds. With brand-new and advanced tracking technology at hand, Chernetsov et al. (2004) obtained very detailed information on the individual migratory directions by deploying the young storks with satellite-tags. Despite all detail, the results could not have been more ambiguous with respect to the presence or absence of innate migratory directions. Chernetsov et al. (2004) concluded that 'in soaring migrants that are heavily dependent on local topography, social contacts and observation of the performance of migrating conspecifics play a much greater role than in nocturnal migrants that usually fly individually.'

We suggest that we cannot exclude this possibility for Perdeck's starlings as well. The case can only be closed with new experiments that include the translocation of completely unexperienced individuals, i.e. starlings that have been raised without any relevant social information. However, completely excluding all social information is harder than it may sound, as specific social circumstances during or even before hatching (e.g. sounds made by the breeding parent, Gottlieb 1976), and subtle social circumstances after hatching (e.g. conspecifics flying overhead) could all potentially influence the development of migratory preferences. Nonetheless, experiments that exclude specific social information will help to position the study of bird migration in the heart of contemporary studies on the role of individual learning (Gottlieb 2002) in relation to various forms of transgenerational information exchange in adaptation and evolution (Jablonka and Lamb 2014, Laland et al. 2015). For now, the question of whether the preferred migratory direction of Perdeck's displaced young starlings involved learning, or did not, is as open as it was in 1958.

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Supplementary material (available online as Appendix jav-02337 at <www.avianbiology.org/appendix/jav-02337>). Appendix 1–2.

Appendix 1. Review of the quotes in 12 books on bird migration based on Perdeck (1958) and whether they attributed, either directly or indirectly, an existence of innate migratory directions to the experiments reported in this publication. For the latter two categories the relevant sentences are highlighted in red.

Book	Pages	Citation content to Perdeck 1958	Innate interpretation	Attribution to Perdeck 1958
Drost, J. 1962. The migrations of birds. Heinemann, London.	330-333	"The young… kept their main south-west direction, and flew to southern France and the Iberian peninsula.... Adults … returned to their customary winter area by flying north-west, a very different direction from that of their normal migration. Even more curious, young starlings left the next spring to breed in their original territory, but returned the following autumn to winter where they had gone the preceding year after their displacement."	No	
Matthews, G. V. T. 1968. Bird navigation, Second Edition. – Cambridge University Press, London.	10-15	"In those species where the young migrate independently of the old we have a natural experiment showing that any tendency to fly in one direction must be part of the bird's innate behaviour, the Cuckoo provides an extreme example. **Where young and old migrate together the former could possibly *learn* the migration direction as well as the final location of the wintering area**. This can be tested by holding young birds in the area of their breeding until all others of their species have departed." "The young birds [of Perdeck 1958] continued to migrate from the release point in that direction which their congeners follow from the trapping point."	No	

Schüz, E., Berthold, P., Gwinner, E. and Oelke, H. 1971. Grundriss der Vogelzugskunde. – Verlag Paul Parey, Berlin.	299-301	"Die meisten Jungstare wandten sich nach Sudfrakreich , manche bis nach SW-Panien. Die Altvogel hingegen schlugen eine neue Richtung ein: Die Wiederfunde streuen un eine von SE nach NW verlaufende Linie, die den Auflassungsort mit den normalen Winterquartier verbindet. Einige der wiedergefundenden Altstare hatten ihr normales Winterquartier sogar erreicht. ... Den Jungstaren hingegen fehlt offensichtlich die Landkarte. Sie scheinen nur uber einer Kompass zu verfugen, der ihnen erlaubt, eine vorgegegene Richtung einzuhalten."	No	
Baker, R. R. 1978. The evolutionary ecology of animal migration. – Hodder and Stoughton, London.	610-611, 912-913	"Evidence is also accumulating that not only the direction but also the distance of autumn migration in juveniles is endogenously determined. Two types of evidence are available that tend to support this hypothesis, one type coming from displacement experiments and the other from an apparent correlation between zugunruhe and migration distance" "[based on Perdeck 1958:] The results are consistent with the thesis that the first autumn migration of young starlings is exploratory but with an endogenously determined bias to the direction ratio."	**Yes**	direct
Mead, C. 1983. Bird migration. – Country Life Books, Feltham.	140-141	"The adult birds invariably started to make their way north-west to the area where they had presumably wintered in earlier years. The young birds carried on to the south-west and ended up in a wintering area which their part of the European-breeding population would seldom, if ever, reach."	No	

Alerstam, T. 1990. Bird migration. – Cambridge University Press, Cambridge.	374-376	"Perdeck drew the conclusion that Starlings over one year old use navigational migration to return to their traditional winter quarters. Young Starlings which have never before been in the winter quarters, by contrast use orientational navigation." (p. 376). Earlier, on p. 374 orientational navigation is defined as "the birds have an innate directional instinct which leads them in the right way between summer quarters and winter quarter"	**Yes**	indirect
Burton, R. 1992. Bird migration. – Aurum Press, London.	66-67	"No matter whether they were released singly or in flocks, the adults readjusted their course and headed north-west to be caught later on their normal wintering grounds. The inexperienced starlings continued on the same south-west course as they had been taking along the eastern coast of the North Sea. .... This is evidence that young birds merely fly on a fixed, presumably genetically coded, heading until some signal, either internal or from the environment, or a combination of two, tells them that they have gone far enough."	Yes	direct
Berthold, P. 1993. Bird migration. A general survey. – Oxford University Press, Oxford.	140-144	"Juveniles on their first migration subsequently migrated parallel to their original migratory direction, thus reaching Spain, a destination not normally reached by this population. These birds obviously followed a given compass direction, and did not take into account the displacement." "Innate migratory directions can also be inferred from displacement experiments. The most impressive experiment of this kind was conducted by Schüz on White storks. From East Prussia 144 eastern migrants were transported across the European migration divide to the region of western migrants and released their after the local birds had	Yes	direct

		left. Most of the test birds set off in the eastern direction typical for them. When the eastern storks were released before the local birds had left, a large proportion of the birds joined the western migrants. in this case their innate goal direction was modified by social bonds."		
Berthold, P. 1996. Control of bird migration. – Chapman and Hall, London.	244-247	With implicit reference to Perdecks 1958 results presented in Fig. 3.1: "Inexperienced individuals of many species that normally migrate alone are able to fly fixed courses ("normal directions") in order to reach species-specific wintering areas. This directional or compass orientation is based on preprogrammed directions." "Compass orientation (flying innate courses) in naive migrants and true navigation based on gradient maps in experienced birds... may, then, be the two basic orientation mechanisms of avian migration. Preprogrammed compass orientation could also be used in experienced birds.	Yes	direct
Berthold, P. 2001. Bird migration. A general survey, Second edition. – Oxford University Press, Oxford.	143-146	Repeat of texts in edition of 1993	Yes	direct
Newton, I. 2008. The migration ecology of birds. – Academic Press, London.	234-236	"The subsequent ring recoveries from translocated juveniles were on a line west-southwest of the release site and extended for a similar distance as usual (into southern France and northern Iberia). This indicated that the translocated juveniles had kept their inherent directional preference and normal migration distance, but not corrected for displacement."	Yes	direct

Newton, I. 2010. Bird migration. – HarperCollins, London.	228-229	"The subsequent ring recoveries from translocated juveniles were on a line west-southwest of the release site and extended into southern France and northern Iberia. This indicated that the translocated juveniles had kept their inherent directional preference and normal migration distance, but had not corrected for displacement."	Yes	direct

Appendix 2. Review of the journal citations to Perdeck (1958) and whether or not they attributed an existence of innate migratory directions either directly or indirectly to the experiments reported in this publication. For the latter two categories the relevant sentences are highlighted in red, with the most loaded statements indicated in bold.

	Type	Citation content to Perdeck 1958 (References in content are listed below this table)	Innate interpretation	Attribution to Perdeck 1958
Williamson, K. 1969. Weather systems and bird movements. – Quart. J. Met. Soc. 95: 414-423.	Review	"Perdeck (1958) postulated the existence of a marked dichotomy in the navigational powers of adult Starlings *Sturnus vulgaris* and young of the year. Large samples of a population which migrates regularly from eastern Europe to the British Isles were trapped and ringed in Holland and displaced by aircraft to Switzerland for release. The adults (and juveniles accompanying adults, when released together) corrected for the displacement, being recovered in Britain or at points along the new route, thus showing a 'goal orientation.' Young birds released alone, however, were recovered at places farther west than the release-point, in south France and north Spain, in territory quite unknown to the population in question, thus showing a ' one-directional ' orientation."	No	
Wolff, W.J. 1970. Goal orientation versus one-direction orientation in Teal *Anus c. crecca* during autumn migration. – Ardea 58: 131-141.	Topical	"Perdeck (1958) proved that the juveniles of this species continued to migrate in the direction they did before they were displaced, and that the adults changed their direction and went to their familiar winter quarters."	No	
Trivers, R.L. 1971. The evolution of reciprocal altruism. – Q. Rev. Biol. 46: 35-57.	Review	"There do exist data suggesting that close kin in a number of species migrate or disperse great distances from each other (Ashmole 1962, Perdeck 1958)"	No	
Schmidt-Koenig, K. 1973. Über die navigation der vögel. – Naturwissenschaften 60: 88-94.	Review	"Zahlreiche Versuche, bei denen Zugvögel beringt underst nach Verfrachtung freigelassen worden waren, zuletzt von Perdeck (1958), stimmten in einem überein: Altvögel navigieren zum angestammten Wintergebiet, sie kompensieren die	No	

		Verfrachtung; Jungvögel, die sich auf ihrem ersten Herbstzug befinden, ziehen parallel zum angestammten Kurs weiter. Sie bringen offenbar eine Information über die Richtung mit, in die sie ziehen müssen."		
Able, K.P. 1977. Orientation of passerine nocturnal migrants following offshore drift. – The Auk 94: 320-330.	Topical	"The classic studies of Perdeck (1958, 1967) indicated that juvenile birds making their first autumn migration employed only compass direction and distance components. In contrast to adults, they seemed unable to compensate for longitudinal displacements."	No	
Burt, H.E. and Giltz, M.L. 1977. Seasonal directional patterns of movements and migrations of starlings and blackbirds in North-America. – Bird-Banding 48: 259-271.	Topical	"Perdeck (1958) **cites** displacement experiments in the fall in which young Starlings continued to the southwest. Kramer (1951), recording the Zugunruhe of Starlings in October, found their orientation was to the southwest and in the spring the orientation was northeast for at least 10 days. So, possibly some Starlings with this genetic orientation were among those imported to this country around 1890."	**Yes**	Indirect
Gwinner, E. 1977. Circannual rhythms in bird migration. – Ann. Rev. Ecol. Syst. 8: 381-405.	Review	"Comparable results suggesting the participation of endogenous time factors in the control of fall migration of first year European starlings were obtained by Perdeck (1958, 1964)."	**Yes**	Direct
Rabøl, J. 1978. One-direction orientation versus goal area navigation in migratory birds. – Oikos 30: 216-223.	Review	"At the time of my first displacement experiments (Rabøl 1969) it was generally supposed, mainly on the basis of the starling displacement experiments by Perdeck (1958, 1967), that the migratory route of a juvenile bird was inherited as a programme for one-direction (compass) orientation."	**Yes**	Direct

Wiltschko, W. and Wiltschko, R. 1977. A theoretical model for migratory orientation and homing in birds. – Oikos 30: 177-187.	Review	"The large scale displacement experiments of Perdeck (1958, 1967) clearly demonstrated that young birds on their first migration did not compensate for the displacement and thus apparently do not fly towards a goal, but on a standard direction. Many hand-raised birds isolated from adults showed in cages directional tendencies coinciding closely with the migratory directions of their free-living conspecifics, (e.g. Sauer 1957, Hamilton 1962, Emlen 1972, Wiltschko and Gwinner 1974) indicating that the information of the migratory direction is indeed innate." "The banding recoveries of starlings *Sturnus vulgaris* displaced during autumn migration (Perdeck 1958, 1967) showed that the juvenile birds continued over a distance more or less comparable to that between the trapping place and the normal winter quarters. This was also true when they had been released in a region which served as winter quarters for other populations of their conspecifics (Perdeck 1967) indicating that they have some innate information about the distance of their migration. This information may be provided by an endogenous time program (Gwinner 1974). Gwinner (1968) found that the amount of Zugunruhe of closely related species is correlated with their distance of migration and that the Zugunruhe of hand-raised birds in their first autumn is dimensioned so that it will make the birds reach their normal wintering range."	**Yes**	Indirect
Alerstam, T. 1979. Wind as selective agent in bird migration. – Ornis Scand. 1: 76-93.	Topical	"I will assume that the migrants are able to determine the direction towards their goal and by way of redetermination of this direction will reach the goal in spite of geographical displacement (this is to say that the migrants are capable of true navigation). However, such a navigational capacity may be an u realistic assumption for many birds, particularly for juveniles on their first autumn migration (Perdeck 1958, 1967) which probably use compass (one-direction) orientation in combination with an endogenous seasonal clock (Gwinner 1975)."	**Yes**	Indirect

Baker, R.R. 1980. The significance of the Lesser Black-backed Gull to models of bird migration. – Bird Study 27: 41-50.	Topical	"There are two other extant models of bird migration: the clock-and-compass model (Perdeck 1958, Dorst 1962), and the goal-area navigation model (Rabol 1970, 1978). According to the clock-and-compass model, a young bird migrates for a fixed time in a fixed direction (time and direction being innately programmed). It then settles and feeds up before repeating the entire process a fixed and programmed number of times."	**Yes**	Direct
Wiltschko, W., Gwinner, E. and Wiltschko, R. 1980. The effect of celestial cues on the ontogeny of non-visual orientation in the Garden Warbler (*Sylvia borin*). – Z. Tierpsychol. 53: 1-8.	Topical	"Some experiments indicate that these young birds possess innate information about the distance (Gwinner 1968, for review see: Gwinner 1977) and direction of their migratory flight (Perdeck 1958, for review see: Walraff 1977, Wiltschko 1977)."	**Yes**	Direct
Cave, A.J. 1982. Experiments on the use of the sun by Starlings in the discrimination of geographical locations for navigation. – Ardea 70: 197-216.	Topical	"Perdeck (1958) …. Showed that during autumn migration adult Starlings are able to compensate for an experimental sideways displacement by means of goal orientation towards their winter quarters. Juveniles did not compensate during autumn migration, but moved in a normal autumn direction, apparently using one-direction orientation."	No	
Roitblat, H.L. 1982. The meaning of representation in animal memory. – Behav. Brain Sci. 5: 353-406.	Review	"Other experiments on animal navigation also suggest that animals use experience-derived models of their environment to control behavior. For example, displacement studies with migrating Starlings (e.g., Perdeck 1958) show that experienced birds use some kind of map of their migratory route (perhaps referred to solar or stellar coordinates) to control their flight path. Perdeck captured Starlings in Holland during their autumnal migration from Eastern Europe and displaced them by air to Switzerland, where they were released. Adult Starlings compensated for this displacement and flew in a northwesterly direction, ending in their usual wintering ground. Juveniles (birds who had never migrated before), in contrast, did not	No	

		compensate for the displacement and continued in the same direction they had been flying before capture, ending their migration in an area where others from their breeding population were not found (though starlings from other summering locations were found in that area), and continuing to winter there in subsequent years."		
Kiepenheuer, J. 1984. The magnetic compass mechanism of birds and its possible association with the shifting course directions of migrants. – Behav. Ecol. Sociobiol. 14: 81-99.	Topical	“At least the fall migrating direction is innate it is followed by young birds even when not accompanied by adults or parents (Schüz 1949, Perdeck 1958 and others).”	**Yes**	direct
Moore, F.R. 1984. Age-dependent variability in the migratory orientation of the Savannah Sparrow (*Passerculus sandwichensis*). – Auk 101: 875-880.	Topical	"Although the direction (Gwinner and Wiltschko 1978, 1980) and distance (Berthold and Querner 1981) of their first autumnal migration may be endogenously determined, naive birds have no information about their route or final destinations at the time they initiate migration. The high within-individual variability and the lack of clear between-individual differences among the inexperienced Savannah Sparrows are consistent with this notion (see: DeSante 1983). Only after an individual becomes familiar with an area can site-specific information be used to determine the direction towards a goal (see: Wiltschko and Wiltschko 1982). Experience is likely to be important in any process whereby migrants "attach" themselves to their wintering grounds and possibly *en route* locations (see: Perdeck 1958, 1967)”	**No**	
Able, K.P. and Bingman, V.P. 1987. The development of orientation and navigation behaviour in birds. – Q. Rev. Biol. 62: 1-29	Review	"More specific differences between the behavior of experienced and inexperienced birds have been revealed by displacement experiments, such as those performed with European Starlings (*Sturnus vulgaris*) by Perdeck (1958, 1967). These classic studies have been reviewed by Emlen (1975), Able (1981), and others; here a brief	**Yes**	Indirect

		summary will suffice. A large number of hatching year and adult starlings were captured on migration and displaced from the Netherlands to Switzerland. Recoveries during the subsequent winter showed that the young, inexperienced birds exhibited no evidence of recognition of their displacement and migrated in a SW direction toward Spain. Experienced adults, on the other hand, corrected for the displacement and instead of flying on their usual SW track, headed primarily NW back toward the wintering ground occupied by their population. These and subsequent displacement experiments showed rather convincingly that on its first autumn migration, a young starling has knowledge of the direction and perhaps approximate distance to the winter range of its population, but no specific information about the coordinates of that goal. Thus, if displaced, it cannot perform a navigational correction and cannot reach the wintering ground it has never visited. Gwinner (see: 1977), Berthold (1978), and Gwinner and Wiltschko (1978) present evidence that distance and direction values are genetically programmed to a degree sufficient to allow a first-time migrant to perform adequately this "vector-navigation"		
Neusser, V.E. 1987. Richtungsbevorzugungen von Mönchsgrasmücken (*Sylvia atricapilla*) während der Herbstzugunruhe vergleich zweier populationen mit verschiedenen zugrichtungen. – Ethology 74: 39-51.	Topical	"Auch die Ergebnisse einiger Verfrachtungsversuche mit Buchfinken (*Fringilla coelebs*; Perdeck 1958), Nordamerika-Krahen (*Corvur bruchyrhynchos*; Rowan 1946) und Sperbern (*Accipiter nisus*; Drost 1938) sind am besten mit der Annahme genetisch festgelegter Zugrichtungen zu erklaren."	**Yes**	Direct
Wiltschko, W. and Daum, P. 1987. The development of the star compass in Garden Warblers, *Sylvia borin*. – Ethology 74: 285-292.	Topical	"Large-scale displacement experiments (Perdeck 1958, 1964) have shown that they possess genetically transmitted information on the direction and distance of their migratory route."	**Yes**	Direct

Baldacinni, N.E. and Bezzi, E.M. 1989. Orientational responses to different light stimuli by adult and young sedge warbler (*Acrocephalus schoenobaenus*) during autumn migration: a funnel technique study. – Behaviour 110: 1-4.	Topical	"Such a complex integration of several reference systems certainly necessitates a process of biological maturation, or learning, during the first migratory cycle, as has been demonstrated by Perdeck's pioneer work (1958) on starlings."	No	
Green, R.E., Hirons, G.J.M. and Johnson, A.R. 1989. The origin of long-term cohort differences in the distribution of Greater Flamingos *Phoenicopterus ruber roseus* in winter. – J. Anim. Ecol. 58: 543-555.	Topical	"Individual differences between young birds in the use of particular staging areas may persist throughout life (Perdeck 1958, Townshend 1982), importance of environmental factors, relative to inheritance and cultural determining these differences has not been assessed."	No	
Wiltschko, R. 1989. Aus der geschichte der orientierungsforschung. – J. Ornithol. 130: 399-421.	Review	"Besonders bemerkenswert sind die Verfrachtungen der Vogelwarte Helgoland mit Sperbern, die in Schlesien aufgelassen wurden, denn die Verteilung der wenigen Wiederfunde fuhrte Drost (1938) zu den gleichen Schlulgfolgerungen, die Perdeck (1958) 20 Jahre spater aus dem wesentlich grosseren Material seiner beruhmtgewordenen Staren versuche ziehen sollte, namlich, dass junge Vögel auf dem ersten Zug bestimmte Kompassrichtungen fliegen, wahhrend erfahrene Vögel, die schon ihr traditionellen Winterquartier uberwintert haben, dieses gezielt ansteuern konnen."	No	
Berthold, P. 1990. Spatiotemporal programs and genetics of orientation. – Experientia 46: 363-371.	Review	"Young European starlings (*Sturnus vulgaris*) trapped in the Netherlands during their autumn migration from the Baltic region to west European wintering areas and transferred to (and released in) Switzerland, continued their autumn migration to Spain, an area that normally is not reached. Thus, they continued their migratory journey in the programmed direction and to some extent also for the expected	**Yes**	Direct

		distance in spite of the transfer (Perdeck 1958). Empirical support for the existence of endogenous, spatial orientation-programs comes also from a detailed analysis of directional preferences in garden warblers."		
Ens, B., Piersma, T., Wolf, W.J. and Zwarts, L. 1990. Homeward bound: problems face when migrating from the Banc d'Arguin, Mauritania, to their northern breeding grounds in spring. – Ardea 78: 1-16	Review	"In addition, juveniles of a species may have a programmed migration distance (Berthold 1973), as well as a programmed migration direction (Perdeck 1958)"	**Yes**	Direct
Richardson, W.J. 1990. Wind and orientation of migrating birds: a review. – Experientia 46: 416-425	Review	"However, this would require an ability to detect and correct for previous displacement from the straight-line route. It is not clear how many birds have this ability, especially in the case of juveniles *en route* to the wintering grounds for the first time (Emlen 1975, Perdeck 1958)."	No	
Walraff, H.G. 1990. Conceptual approaches to avian navigation systems. – Experientia 46: 379-388	Review	"Perdeck conducted an experiment which has meanwhile become a classic. More than 11,000 starlings, caught during migration in Holland, were transported to and released in Switzerland. Distributions of recovery sites in the subsequent winter months met both possible expectations, depending on the age of the birds (Fig. 1): 1) Young starlings, migrating for the first time, when displaced perpendicularly to the compass direction normally taken by the population, continued to fly this normal compass course and hence arrived in an abnormal area dislocated by approximately the direction and distance of displacement. 2) Older starlings, which had spent a winter in the population- specific area at least once, flew an abnormal compass direction leading them toward the normal (already familiar) wintering area." "The result obtained with the young starlings suggests two conclusions: a) Some environmental references were apparently available in Holland as well as in	**Yes**	Direct

		Switzerland according to which an identical compass course could have been chosen, b) The birds apparently followed some 'internal command' to select just one specific course angle an intended direction with regard to this reference(s)."		
Helbig, A.J. 1991. Inheritance of migratory direction in a bird species: a cross-breeding experiment with SE- and SW-migration Blackcaps (*Sylvia atricapilla*). – Behav. Ecol. Sociobiol. 28: 9-12	Topical	"A classic large-scale displacement experiment with starlings (*Sturnus vulgaris*) demonstrated among other things that juveniles on their first migration possess no knowledge about the geographic coordinates of the wintering area (Perdeck 1958). There is substantial evidence that such inexperienced migrants rely largely on innate information about distance and direction in which to migrate. An approximate measure of distance is encoded in an endogenous circannual programme as the duration of migratory activity per season (Gwinner 1968, Berthold 1973)."	**Yes**	Indirect
Schwabl, H., Gwinner, E., Benvenuti, S. and Ioale, P. 1991. Exposure of Dunnocks (*Prunella modularis*) to their previous wintering site modifies autumnal activity pattern: evidence for site recognition? – Ethology 88: 35-45.	Topical	"Displacement experiments during or after autumn migration do indeed indicate that birds learn aspects of their wintering sites so that they can "home" successfully to these areas after displacement (Perdeck 1958, 1967)."	No	
Berthold, P., Helbig, A.J., Mohr, G. and Querner, U. 1992. Rapid microevolution of migratory behaviour in a wild bird species. – Nature 360: 668-670.	Topical	“homing towards familiar winter quarters as demonstrated in displacement experiments with starlings”	No	
Alerstam, T. 1996. The geographical scale factor in orientation of migrating birds. – J. Exp. Biol. 199: 9-19.	Review	"On a larger scale, we do not know whether birds use any means of orienting along the shortest great circle routes, and we are uncertain whether a ‘vector orientation’ mechanism (an inherited orientation programme based on a succession of vectors	**Yes**	Indirect

		with directions and lengths as defined by constant compass courses in force for different seasonal periods according to an endogenous circannual clock, cf. Gwinner and Wiltschko 1978, 1980) is sufficient to guide the birds between breeding and winter quarters (Kiepenheuer 1984). Are elements of coordinate determination or goal area navigation (Rabøl 1978, 1985) involved in the migratory orientation, perhaps playing different roles for adult and juvenile birds (see: Perdeck 1958)?"		
Helbig, A.J. 1996. Genetic basis, mode of inheritance and evolutionary changes of migratory directions in palearctic warblers (Aves: *Sylviidae*). – J. Exp. Biol. 199: 49-55.	Topical	"In a classic field experiment, several thousand European starlings *Sturnus vulgaris* were displaced from autumn stopover sites in Holland perpendicular to the expected migration route (Perdeck, 1958). The results have been comprehensively illustrated by Emlen (1975). Juvenile starlings, ringed and released singly after an 800 km aeroplane flight, continued to migrate from the release site in approximately the same direction as they had flown prior to displacement, i.e. west-southwest. Adults, however, compensated for the displacement by migrating northwest towards the winter quarters in northern France and southern England, where they had spent at least one previous winter."	No	
Munro, U., Munro, J.A. and Phillips, J.B. 1997, Evidence for a magnetite-based navigational "map" in birds. – Naturwissenschaften 84: 26-28.	Topical	"Juvenile migrants heading towards still unfamiliar winter quarters rely exclusively on an innate migration program that provides the compass course of their migration (Berthold 1988). In contrast, adult birds which have already spent considerable time in their overwintering area incorporate information which they have learned during previous migrations into their orientation system. This leads to the development of a navigational "map" (Kramer 1957) which enables the birds to determine the compass course towards their goal by mechanisms of true navigation (Perdeck 1958)."	**Yes**	Indirect
Mouritsen, H. and Larsen, O.N. 1998. Migrating young pied flycatchers *Ficedula hypoleuca* do not compensate for geographical	Topical	"What are the spatiotemporal orientation programmes (see e.g. Berthold 1991, Mouritsen 1998, 1999) and reaction patterns of young night-migrating passerines over the course of their first migratory season?" "Perdeck's (1958) impressive displacement experiment using European starlings *Sturnus vulgaris* is the classic	**Yes**	Indirect

displacements. – J. Exp. Biol. 201: 2927-2934.		textbook experiment, which provides convincing evidence that young European starlings use a simple clock-and compass strategy, whereas adult European starlings seem to have acquired navigational abilities through associative learning and experience."		
Wehner, R. 1998. Navigation in context: grand theories and basic mechanisms. – J. Avian Biol. 29: 370-386.	Review	"These experimental findings - together with some earlier displacement experiments performed with White Storks (Schüz 1951) and Common Starlings Sturnus vulgaris (Perdeck 1958, 1967) - clearly show that at least some migratory birds are endowed with endogenous vector programmes"	**Yes**	Direct
Able, K. P. 2000. The concepts and terminology of bird navigation. – J. Avian Biol. 32: 174-183.	Review	"Without prior migratory experience, the young birds could only proceed in the direction and for the distance dictated by vector navigation. In species that migrate in social groups, the coded direction of vector navigation may be influenced by the behavior of other flock members"	**Yes**	Direct
Schmidt-Koenig, K.S. 2001. Zur Geschichte der orientierungsforschung. – J. Ornithol. 142: 112-123.	Review	"Der holländische Ornithologe A. C. Perdeck (1958) hat sie genutzt und an groβem Datenmaterial bewiesen, was sich in den Versuchen an der Vogelwarte Rossitten bereits abgezeichnet hatte (Abb. 1): Vögel verffigen tiber mindestens zwei verschiedene Orientierungsverfahren. Altvögel, die schon wenigstens einen Weg- und Heimzug geleistet hatten, waren zu dem fähig, was ,,echte Navigation" genannt werden kann. Sie flogen von ihnen unbekannten Orten zum angestammten Uberwinterungsgebiet. Junge Vögel, die sich auf dem ersten Herbstzug ihres Lebens befanden, verfügten über die später so genannte Vektornavigation, ein Verfahren, das mit zwei genetisch programmierten, populationsspezifischen Komponenten arbeitet. Die eine ist eine Information über die Zugrichtung, die zweite ist eine Information über die Zugentfernung."	**Yes**	Direct
Bäckman, J. and Alerstam, T. 2003. Orientation scatter of free-flying nocturnal passerine migrants:	Topical	"Juveniles are thought to orient according to an inherited vector program (Gwinner and Wiltschko 1978, Berthold 1991), unable to make adjustments for artificial	**Yes**	Indirect

components and causes. – Anim. Behav. 65: 987-996.		displacements during the journey, but adult birds may have learned cues that are used for true navigation (Perdeck 1958)."		
Hake, M., Kjellen, N. and Alerstam, T. 2003. Age-dependent migration strategy in honey buzzards *Pernis apivorus* tracked by satellite. – Oikos 103: 385-396.	Topical	"The adults presumably have learnt cues which make it possible for them to correct for the displacement associated with the detour and navigate back to their previous winter sites after reaching West Africa (Perdeck 1958). In contrast, the juveniles may be constrained by their endogenous spatiotemporal migration programme (Gwinner 1996)"	**Yes**	Indirect
Mettke-Hofmann, G. and Gwinner, E. 2003. Long-term memory for a life on the move. – PNAS 100: 5863-5866.	Topical	"It is known from several in-depth studies that young passerines on their first migration use the sun, the stars, and or the earth's magnetic field as compasses to guide them into appropriate, presumably innate directions (Kramer 1951, Emlen, 1967, Wiltschko and Wiltschko 1988). The distance, and thus the endpoint of migration, appears to depend, at least in part, on an endogenous circannual program (Gwinner 1986). However, there is also evidence that this simple system of ‘‘vector navigation’’ is supplemented or replaced in older birds by more complex navigation systems that are based on learning (Perdeck 1958).	**Yes**	Indirect
Thorup, K., Alerstam, T., Hake, M. and Kjellen, N. 2003. Bird orientation: compensation for wind drift in migrating raptors is age dependent. – Biol. Lett. 270: 8-11.	Topical	"One may speculate that juveniles migrating in mixed flocks with adults benefit from the compensatory ability of the adults. The reason for the age-dependent difference in compensatory ability may be related to the possible availability of acquired map information, allowing experience adults to detect and correct for lateral displacement, whereas juveniles on their first migratory journey may be more restricted to simple vector orientation, as indicated by classical displacement experiments with migratory sparrow hawks, starlings and chaffinches (Drost 1938, Perdeck 1958, Berthold 2001)."	No	
Wiltschko, R. and Wiltschko, W. 2003. Avian navigation: from	Review	"Another common characteristic of homing and migratory orientation is the change in strategy with increasing experience, which mainly concerns the mechanisms providing the compass course (e.g. Perdeck 1958, Wiltschko and Wiltschko 1985).	**Yes**	Indirect

historical to modern concepts. – Anim. Behav. 65: 257-272		Navigation by young, inexperienced birds must be based on innate mechanisms, **because other mechanisms are not yet available**."		
Chernetsov, N., Berthold, P. and Querner, U. 2004. Migratory orientation of first-year white storks (*Ciconia ciconia*): inherited information and social interactions. – J. Exp. Biol. 207: 937-943.	Topical	"It was expected that the displaced birds, if capable, would follow their innate migratory direction in spite of the displacement (Perdeck 1958)."	**Yes**	Direct
Simons, A. M. 2004. Many wrongs: the advantage of group navigation. – Trends Ecol. Evol. 19: 453-455	Review	"Variation in navigational abilities among individuals is expected, and has several sources. For example, adult and juvenile raptors differ in their ability to compensate for wind drift (Thorup et al. 2003). Similarly, naive migrants might orient correctly (Perdeck 1958), but only experienced individuals can adjust this vector navigation if displaced from the correct route. When differences in ability are recognized by fellow flock members, navigational responsibility might be weighted unequally among individuals."	No	
Bingman, V.P. and Chan, K. 2005. Mechanisms of animal global navigation: comparative perspectives and enduring challenges. – Ethol. Ecol. & Evol. 14: 295-318.	Review	"By contrast, subsequent recoveries of first-year birds with no previous migratory experience tended to cluster in regions in a direction from the release site that would have corresponded to the direction they would have flown if they had not been displaced. That is, they continued to fly the vector they were executing, a signature of vector navigation." "Developmentally, representational mechanisms that support true navigation in migratory birds are thought to build from the baseline of inherited vector navigation (Perdeck 1958, Wiltschko and Wiltschko 2003)."	**Yes**	Direct
Erni, B., Liechti, F. and Bruderer, F. 2005. The role of wind in passerine autumn migration between Europe	Topical	"The existence of an endogenous (genetically determined) direction has been confirmed in many bird species (Wiltschko and Wiltschko 2003, and references therein). It can be assumed that most migrating passerine species have a genetically	**Yes**	Direct

and Africa. – Behav. Ecol. 16: 732-740.		inherited migratory direction (Berthold 1996) and rely on this direction for a given time period, especially during their first autumn migration (Mouritsen 1998, Perdeck 1958)."		
Alerstam, T., Hake, M. and Kjellen, N. 2006. Temporal and spatial patterns of repeated migratory journeys by ospreys. – Anim. Behav. 71: 555-566.	Topical	"adult birds but not juveniles often tend to correct for the displacement. However, their homing seems to be directed towards the winter destinations rather than towards sites along their migration routes."	No	
Holland, R.A., Wikelski, M. and Wilcove, D.S. 2006. How and why do insects migrate. – Science 313: 794-796	Review	"In the case of migrating birds, a species-specific wintering ground is usually the goal, and it is located by an endogenous program of vector navigation in the first migratory journey, and possibly by ‘‘true navigation’’ based on experience in subsequent years (Perdeck 1958)."	**Yes**	Direct
Liechti, F. 2006. Birds: blowin' by the wind? – J. Ornithol. 147: 202-211.	Review	"Juveniles, as probably vector-oriented individuals, did not compensate for lateral wind drift, while adults, as goal-oriented migrants, compensated partially for lateral wind drift, as would be expected in an adaptive drift strategy. This result, which is in line with Perdeck's (1958) famous experiments with starlings, indicates that juveniles might actually be unable to adopt a goal-oriented adaptive drift strategy."	No	
Åkesson, S. and Bianco, G. 2017. Route simulations, compass mechanisms and long-distance migration flights in birds. – J. Comp. Physiol. A. 203: 475-490.	Topical	"observations from both juvenile and adult birds, or a combination of both, for which the ability to navigate may be questioned in juvenile birds (e.g., Perdeck 1958)" [1]	No	

Pulido, F. 2007. The genetics and evolution of avian migration. – BioSchience 57: 165-174.	Review	"Large-scale displacement experiments with starlings (Sturnus vulgaris) and other species, and analyses of ringing recoveries, suggest that the wintering area used by a bird in its first year—that is, the area chosen after the first migratory journey—is also used in subsequent seasons (Perdeck 1958, Mouritsen 2003). Thus, the first migratory trip, as determined by the genetic program, determines the wintering site used by each individual bird and each individual's migration. By this mechanism, the genetic program and its variation measured in the laboratory become major determinants of phenotypic variation in migratory behavior and evolutionary processes in the wild."	**Yes**	Direct
Thorup, K., Bisson, I.-A., Bowlin, M. S., Holland, R. A., Wingfield, J. C. Ramenofsky, M. and Wikelski, M. 2007. Evidence for a navigational map stretching across the continental U.S. in a migratory songbird. – Proc. Natl. Acad. Sci. USA 104: 18115–18119.	Topical	"In a now classic experiment by Perdeck (1958), 11,000 starlings, *Sturnus vulgaris*, were displaced by airplane from The Netherlands to Switzerland during 1955–1957. Whereas displaced juvenile starlings were recovered in a southwesterly direction (equivalent to the normal migratory direction of the species) toward Spain, adult starlings were recovered in a northwesterly direction toward their known wintering sites in Northwest Europe. **This was interpreted** as showing that juvenile starlings find their species-specific wintering grounds by flying in an inherited direction, whereas adults navigate toward their previously experienced wintering grounds."	**Yes**	Direct
Thorup, K. and Rabøl, J. 2007. Compensatory behaviour after displacement in migratory birds. A meta-analysis of cage experiments. – Behav. Ecol. Sociobiol. 61: 825–841.	Review	"Perdeck (1958) performed an impressive displacement experiment involving more than 11,000 starlings of *Sturnus vulgaris*. The unaltered direction shown by the displaced juvenile birds suggested the use of the simplest vector orientation without compensation in first-time migrants, whereas experienced birds tended to orient back toward the previously experienced wintering site. However**, the starling is a highly social, diurnal, short distance migrant. This means that the result could be influenced by social interactions"**	No	

Chernetsov, N., Kishkinev, D. and Mouritsen, H. 2008. A long-distance avian migrant compensates for longitudinal displacement during spring migration. – Curr. Biol. 18: 188-190.	Topical	"Many displacement experiments have been performed with young birds on their first autumn migration (Mouritsen et al. 2001, Drost 1938, Perdeck 1958, Rüppel 1944, Chernetsov et al. 2004, Thorup and Rabøl 2007). The vast majority of these studies suggest that young birds on their first autumn migration use a very simple spatiotemporal navigation strategy, namely, simple vector navigation, also called the clock-and-compass or, better, the calendar-and-compass strategy (Rabøl 1978, Berthold 1991, Mouritsen and Mouritsen 2000). In contrast to young birds on their first autumn migration, adult birds and young birds returning in spring have personal experience with their goals and might thus use information collected through experience to refine the orientation strategies (Perdeck 1958)."	No	
Fitzgerald, T.M. and Taylor, P.D. 2008. Migratory orientation of juvenile yellow-rumped warblers (*Dendroica coronata*) following stopover: sources of variation and the importance of geographic origins. – Behav. Ecol. Sociobiol. 62: 1499-1508.	Topical	"For instance, Perdeck (1958) displaced banded adult and young starlings (*Sturnus vulgaris*) during fall migration. Adult birds were recovered on their species-specific wintering grounds after the displacement. However, young birds were recovered in areas that indicated they had simply flown in their species specific migratory direction without adjusting for the artificial displacement, suggesting that young starlings cannot compensate for displacement."	No	
Reilly, J.R. and Reilly, R.J. 2008. Bet-hedging and the orientation of juvenile passerines in fall migration. – J. Anim. Ecol. 78: 990-1001.	Topical	"The work of Thorup et al. 2007, together with other investigations conducted subsequent to the original study by Perdeck 1958 (Wiltschko and Wiltschko 1988, Berthold 1990, Helbig 1996, Mouritsen 1998), implies that first-year birds are not goal directed, but rather migrate using vector-navigation based on predetermined directions (tied to celestial and magnetic cues), coupled with a time or distance programme."	**Yes**	Indirect

Holland, R.A., Thorup, K., Gagliardo, A., Bisson, I.A., Knecht, E., Mizrahi, D. and Wikelski, M. 2009. Testing the role of sensory systems in the migratory heading of a songbird. – J. Exp. Biol. 212: 4065-4071.	Topical	"It has been demonstrated that some juvenile songbirds have an inherited species specific compass direction to reach their wintering grounds on their first journey (Berthold 1991). However, this may result in a failure to reach their normal winter range if they are displaced large distances (Perdeck 1958). Adult migratory birds appear to be able to recognise and correct for such displacements, and head back to their normal winter range (Perdeck 1958, Thorup et al. 2007, Chernetsov et al. 2008)."	**Yes**	Indirect
Thorup, K. and Holland, R.A. 2009. Commentary: The bird GPS – long-range navigation in migrants. – J. Exp. Biol. 212: 3597-3604.	Review	"an impressive experiment carried out on starlings by Perdeck (1958). In that study, more than 11,000 starlings caught on migration in The Netherlands were transported to Switzerland and ringed. After release, recoveries of the adult birds were in a north-westerly direction from the release site on the way toward their normal wintering grounds in the south of England and in northwest France whereas juveniles were recovered in southwesterly directions corresponding to the normal direction of migration through The Netherlands (Fig. 1A). The obvious conclusion was that experienced birds homed toward their previously visited winter grounds whereas the young, inexperienced migrants relied on an innate one-direction compass programme."	**Yes**	Direct
Karlsson, H., Henningsson, P., Bäckman, Hedenström, A. and Alerstam, T. 2010. Compensation for wind drift by migrating swifts. – Anim. Behav. 80: 399-404	Topical	"Young and inexperienced birds, which make up part of the sample during the autumn migration, may be less prone or able than adult birds to compensate for wind drift, possibly because they migrate by a comparatively simple 'clock-and-compass' system (Berthold 2001), not allowing correction for geographical displacement to the same extent as the more complex navigation system used by experienced birds (see Perdeck 1958, Åkesson 2003, Thorup et al. 2003, 2007)."	**Yes**	Indirect
Kishkinev, D., Chernetsov, N. and Mouritsen, H. 2010. A double-clock or jetlag mechanism is unlikely to be	Topical	"Moreover, there are other studies in which migratory birds displaced by plane across hundreds and thousands of kilometres were still able to navigate (e.g., Perdeck 1958, Thorup et al. 2007). It means that experienced (non-first autumn)	No	

involved in detection of east-west displacements in a long-distance avian migrant. – Auk 127: 773-780		migratory birds are able to correct for displacement even if they have moved rapidly across time zones."		
Thorup, K., Holland, R. A., Tøttrup, A.P. and Wikelski, M. 2010. Understanding the migratory orientation program of birds: extending laboratory studies to study free-flying migrants in a natural setting. – Integr. Comp. Biol. 50: 315-322	Review	"The migration strategies in birds are commonly (e.g. Berthold 1996) assumed to differ between adult and first-time migrants, in that young birds are guided by a bearing-and-distance program (called a clock-and-compass strategy), whereas adult birds navigate toward the previously visited wintering grounds or breeding grounds. Some very impressive experiments performed by Perdeck (1958, 1964, 1967) and involving displacement of thousands of birds on migration form the basis of this view,"	**Yes**	Indirect
McLaren, J.D., Shamoun-Baranes, J. and Bouten, W. Wind selectivity and partial compensation for wind drift among nocturnally migrating passerines. – Behav. Ecol. 23: 1089-1101.	Topical	"most evidence points to endogenous control being paramount to orientation among juvenile migrants (Perdeck 1958, Thorup et al. 2007, Wiltschko and Wiltschko 2009)."	**Yes**	Direct
Holland, R.A. and Helm, B. 2013. A strong magnetic pulse affects the precision of departure direction of naturally migrating adult but not juvenile birds. – J. R. Soc. Interface 10: 20121047.	Topical	"Evidence suggests that, in the majority of cases, juveniles making their first autumn journey migrate in a population-specific compass direction that is genetically controlled and seasonally appropriate. By contrast, adults additionally call upon a mechanism that allows them to correct for displacements from the normal path (Perdeck 1958, Thorup 2007)."	**Yes**	Direct

Mouritsen, H., Derbyshire, R., Stalleicken, J., Mouritsen, O. Ø., Frost, B.J. and Norris, D.R. 2013. An experimental displacement and over 50 years of tag-recoveries show that monarch butterflies are not true navigators. – PNAS 110: 7348-7353.	Topical	"True navigators not only know which direction to travel (orientation) but also their geographic location in relation to their goal (Gould and Gould 2012, Mouritsen 2013). In other words, they are able to detect both latitude and longitude using a bicoordinate system(Fig. 1A). True navigation has been shown in a variety of taxa, including several species of birds (Perdeck 1958, Chernetsov 2008), the eastern newt (*Notophthalmus viridescens*) (Phillips et al. 1995), the loggerhead sea turtle (*Caretta caretta*) (Putman et al. 2011), and the spiny lobster (*Panulirus argus*) (Boles and Lohmann 2003). Alternatively, some migrants may use a vector (or clock and compass) navigation strategy (Mouritsen 2003, Perdeck 1958, Meyr 1952, Brower 1996, Schmidt-Koenig 1965, Berthold 1991, Mouritsen and Larsen 1998, Mouritsen and Mouritsen 2000), meaning that they do not possess a map but orient in an inherited direction using just a compass system and a clock or calendar (Gwinner and Wiltschko 1978, Munro et al. 1993)."	**Yes**	Indirect
Deutschlander, M.E. and Beason, R.C. 2014. Avian navigation and geographic positioning. – J. Field Ornithol. 85: 111-133	Review	"A classic banding and displacement study of migratory European Starlings by Perdeck (1958) is still one of the most cited references for evidence of map-based navigation by adult migrants. During autumn, thousands of starlings were captured along their migratory route in the Netherlands, banded, and displaced southward to Switzerland. Adults were recovered in their usual population-specific wintering areas in northern France, indicating that they had corrected for the geographic displacement. Juveniles were recaptured southwest of their population-specific wintering grounds (i.e., Spain), showing that juveniles continued to orient in a fixed compass direction without compensation."	No	
Holland, R.A. 2014. True navigation in birds: from quantum physics to global migration. – J. Zool. 293: 1-15.	Review	"Initially, a series of displacement experiments on migrating birds using mark/recapture techniques gathered evidence for true navigation (reviewed in Thorup and Holland 2009). The clearest example (Perdeck 1958) demonstrated that adult but not juvenile birds are capable of migratory true navigation."	No	

Brown, J.M. and Taylor, P.D. 2015. Adult and hatch-year blackpoll warblers exhibit radically different regional-scale movements during post-fledging dispersal. – Biol. Lett. 20150593	Topical	"Prior to moving away from the breeding area, hatch-year birds have no innate knowledge of the geographical area that surrounds them, but do innately know the broad-scale orientation and distance required for their first migratory journey (Mettke-Hofmann and Gwinner 2003, Nisbet et al. 1995)."	**Yes**	Direct
Kishnikev, D. 2015. Sensory mechanisms of long-distance navigation in birds: a recent advance in the context of previous studies. – J. Ornithol. 156: S145-S161.	Review	"Some displacements studies indeed showed that migratory birds gain navigational abilities after their first migration. This indirectly supports the idea that sampling of some spatially distributed natural cues at some sample points is needed to establish a map that could be of magnetic or any other nature (Perdeck 1958, Thorup et al. 2007)."	No	
Wikelski, M., Arriero, E., Gagliardo, A., Holland, R.A., Huttunen, M.J., Juvaste, R., Mueller, I., Tertitski, G., Thorup, K., Wild, M., Alanko, M., Bairlain, F., Cherenkov, A., Cameron, A., Flatz, R., Hannila, J., Hüppop, O., Kangasniemi, M., Kranstauber, B., Penttinen, M., Safi, K., Semashko, V., Schmid, H. and Wistback, R. 2015. True navigation in migrating gulls requires intact olfactory nerves. – Sci. Rep. 5: 17061	Topical	"Migrating birds fly over thousands of kilometres to return to previously visited breeding or non-breeding grounds. Experienced adult birds display the ability to correct for passive displacement from unfamiliar areas (Perdeck 1958), so called true navigation (Griffin 1952, Bingman and Cheng 2006)"	No	

Willemoes, M., Blas, J., Wikelski, M. and Thorup, K. 2015. Flexible navigation response in common cuckoos *Cuculus canorus* displaced experimentally during migration. – Sci. Rep. 5: 16402	Topical	"The complex innate spatio-temporal migration programs, capable of guiding migrant species thousands of kilometres, represents an evolutionary trade-off between species-specific resource needs and movement-related risks, resulting in varying migratory patterns across species and populations (Sutherland 1988, Berthold 2001). The navigational basis of this program is still an unsolved mystery despite decades of research (Alerstam 2006). To investigate the navigational capabilities in birds, experimental displacement is a common practice (Åkesson 2003). Experienced songbird migrants can perform true navigation involving the use of a map sense to identify the position of the current location in relation to a goal, enabling them to compensate for a displacement, even outside familiar areas (Holland 2014). This has been documented using various methods based on migration directions of displaced birds, such as ring recoveries (Perdeck 1958, Mewaldt 1964)"	No
Barkan, S., Roll, U., Yom-Tov, Y., Wassenaar, L.I. and Barnea, A. 2016. Possible linkage between neuronal recruitment and flight distance in migratory birds. – Sci. Rep. 6: 21983.	Topical	"Indeed, several studies have explored the importance of learning and experience for accurate navigation in migratory birds (Perdeck 1958)"	No
Bulte, M., Heyers, D., Mouritsen, H. and Bairlain, F. 2016. Geomagnetic information modulates nocturnal migratory restlessness but not fuelling in a long distance migratory songbird. – J. Avian Biol. 48: 75-82.	Topical	"It is highly likely that the magnetic sense involved here would also be the one involved in sensing position-related information, which experienced birds can use to correct for geographical displacements (Perdeck 1958)"	No

Chernetsov, N.S. 2016. Orientation and navigation of migrating birds. – Biol. Bull. 43: 788-803.	Review	"Since the classic experiments of Perdeck on starlings (*Sturnus vulgaris*) (Perdeck 1958) it is usually assumed that experienced adult migrants performing migration not for the first time use a navigation map, whereas juvenile birds migrating for the first time have no map (in the Northern Hemisphere it usually happens in autumn). It is believed that first-autumn migrants flying towards their winter quarters where they have never been before, do not use a map, which in birds is not innate, but experience-based, but follow an innate spatio-temporal programme (Gwinner and Wiltschko 1978)."	**Yes**	Indirect
Fayet, A. L., Freeman, R., Shoji, A., Boyle, D., Kirk, H.L., Dean, B.J., Perrins, C.M. and Guilfor, T. 2016. Drivers and fitness consequences of dispersive migration in a pelagic seabird. – Behav. Ecol. 27: 1061-1072	Topical	"Migrants with a population-wide single migratory direction are thought to inherit at least the direction and duration of their migration route genetically (Perdeck 1958, Helbig 1991, Berthold et al. 1992, Berthold 1996) or to learn it by following family members or other conspecifics (Chernetsov et al. 2004, Harrison et al. 2010, Palacin et al. 2011)."	**Yes**	Direct
Mouritsen, H., Heyers, D. and Güntürkün, O. 2016. The neural basis of long-distance navigation in birds. – Annu. Rev. Physiol. 78: 133-154.	Review	"Young birds on their first autumn migration use a simple clock-and-compass strategy (also termed the calendar-and-compass strategy or the vector navigation strategy) to locate their wintering grounds (Perdeck 1958, Berthold 1991, Mouritsen and Larson 1998, Mouritsen and Mouritsen 2000, Mouritsen 2003, Holland 2014). Their navigational systems do not involve any map-based feedback but instead work as follows: The birds fly in direction A for X days and then fly in direction B for Y days (although they can deviate from this strategy in some emergency situations, for instance, when they find themselves over water at dawn; see: Mouritsen 2001, 2003). The clock-and-compass strategy requires only an inherited migratory direction, a circannual clock, and at least one compass."	**Yes**	Indirect

Pritchard, D.J., Hurly, T.A., Tello-Ramos, M.C. and Healy, S.D. 2016. Why study cognition in the wild (and how to test it)? – J. Exp. Anal. Behav. 105: 41-55.	Review	"For example, determining whether avian migrants truly know the location of their wintering grounds, rather than just the distance and direction to fly in order to reach them, relies on experiments carried out on a grand scale impossible in the laboratory (Perdeck 1958, Thorup et al. 2007)."	No	
Rotics, S., Kaatz, M., Resheff, Y.S., Feldman-Turjeman, S., Zurell, D., Sapir, N., Eggers, U., Flack, A., Fiedler, W., Jeltsch, F., Wikelski, M. and Nathan, R. 2016. The challenges of the first migration: movement and behaviour of juvenile vs. adult white storks with insights regarding juvenile mortality. – J. Anim. Ecol. 85: 938-947.	Topical	"Previous bird studies showed that migrating juveniles have lower navigation capacity (Perdeck 1967, Thorup et al. 2007, Mueller et al. 2013),"	No	
Brown, J. M. and Taylor, P.D. 2017. Migratory blackpoll warblers (*Setophaga striata*) make regional-scale movements that are not oriented toward their migratory goal during fall. – Move. Ecol. 5: 15	Topical	"Hatch-year individuals, however, likely rely on dead-reckoning, limiting them to genetically-programmed migration routes and limiting their ability to correct for displacement (Perdeck 1958)"	**Yes**	Direct
Finch, T., Butler, S.J., Franco, A.M.A. and Cresswell, W. 2017. Low migratory connectivity is common in long-distance migrant birds. – J. Anim. Ecol. 86: 662-673.	Topical	"Even under relatively deterministic genetic controls, variable weather and wind conditions experienced en route (Elkins 1983), and the varying ability of migrants (and juveniles in particular) to fully compensate for any major displacement from their genetically predetermined migration trajectory (Perdeck 1958, Thorup et al.	**Yes**	Direct

		2003, 2011) will result in deviations, which likely accrue with increasing migration distance."		
Goto, Y., Yoda, K. and Sato, K. 2017. Asymmetry hidden in birds' tracks reveals wind, heading, and orientation ability over the ocean. – Science Adv. 3: e1700097	Topical	"Our results also suggest the high cognitive ability of seabirds to solve an orientation task over the ocean. We could exclude the possibility, known as vector orientation, that the shearwaters continued heading in one particular direction, because turtles and the young birds of some species do (Gaspar et al. 2006, Perdeck 1958, Berthold 2001). For vector orientation, only a sense of direction, that is, the ability to detect direction using a magnetic, sun, or stellar compass, is used. However, more complex orientation ability is required for the flow compensation the shearwaters use to return to their colony after foraging."	No	
Heyers, D., Elbers, D., Bulte, M., Bairlain, F. and Mouritsen, H. 2017. The magnetic map sense and its use in fine-tuning the migration programme of birds. – J. Comp. Physiol. A. 203: 491-497.	Topical	"Indeed, prominent aspects of the birds' migratory programme, such as migratory restlessness behaviour, fuel deposition, and/or directional orientation have been shown to be modified by magnetic fields (Perdeck 1958)"	**Yes**	Indirect
Kishkinev, D., Heyers, D., Woodworth, B.K., Mitchell, G.W., Hobson, K.A. and Norris, D.R. 2017. Experienced migratory songbirds do not display goal-ward orientation after release following a cross-continental displacement: an automated telemetry study. – Sci. Rep. 6: 37326	Topical	"However, Perdeck (1958) found a difference between navigational strategies of first-time and experienced migrants implying that the former were not relying on conspecifics while making navigational decisions, whereas starlings with migratory experience compensated and were found primarily inside their normal wintering area."	**Yes**	Direct

Lundberg, M., Liedvogel, M., Larson, K., Sigeman, H., Grahn, M., Wright, A., Åkesson, S. and Bensch, S. 2017. Genetic differences between willow warbler migratory phenotypes are few and cluster in large haplotype blocks. – Evol. Lett. 1-3: 155-168.	Topical	"Selective breeding and displacement experiments have clearly shown that the migratory behavior in songbirds must be encoded as an innate set of migratory directions and a schedule that provides sufficient information to reach a specific wintering area (Perdeck 1958, Berthold 1990, Helbig 1996).	**Yes**	Direct
Meyburg, B.U., Bergmanis, U., Langgemach, T., Graszynski, K., Hinz, A., Börner, I., Meyburg, C. and Vansteelant, W.M.G. 2017. Orientation of native versus translocated juvenile lesser spotted eagles (*Clanga pomarina*) on the first autumn migration. – J. Exp. Biol. 220: 2765-2776.	Topical	"Outside of the laboratory, the best way to empirically study the role of innate versus external influences on migratory behaviour is through displacement or delayed-release experiments (Perdeck 1958, Schüz 1950)."	No	
Vansteelant, W.M.G., Kekkonen, J., Byholm, P. 2017. Wind conditions and geography shape the first outbound migration of juvenile honey buzzards and their distribution across sub-Saharan Africa. – Proc. R. Soc. B. 284: 20170387	Topical	"Such unexperienced migrants are assumed to follow an innate migratory heading for a predetermined amount of time during one or more bouts of migratory flight (Åkesson and Hedenström 2007, Wiltschko and Wiltschko 2015), which explains why young and inexperienced migrants are often observed not to compensate for wind drift (Thorup et al. 2003, Richardson 1990, Liechti 2006, Alerstam 1979) or experimentally induced displacements (Perdeck 1958), and which suggests they only manage to settle wintering territories if they do not drift too far from suitable habitat."	**Yes**	Indirect
Berdahl, A.M., Kao, A.B., Flack, A. Westley, P.A.H., Codling, E.A.,	Review	mechanism: social learning (experiment with starlings)	No	

Couzin, I.D., Dell, A.I. and Biro, D. 2018. Collective animal navigation and migratory culture: from theoretical models to empirical evidence. – Phil. Trans. R. Soc. B 373: 20170009				
Mouritsen, H. 2018. Long-distance navigation and magnetoreception in migratory animals. – Nature 558: 50-59.	Review	"Inexperienced bird migrants **usually follow experienced companions** or rely on a simple clock-and-compass strategy (vector navigation) using only an innate circannual clock and compass orientation programmes, but no map. They are therefore, except for a few emergency plans, unable to correct for geographical displacement (Mouritsen 2003, 2015, Holland 2014, Perdeck 1958, Chernetsov et al. 2017, Mouritsen and Mouritsen 2000, Deutschlander et al. 2012, Holland and Helm 2013). " "Simple, compass-based, vector orientation relying on an inherited initial direction (Berthold 1999, Mouritsen 2003, Brower 1996, Mouritsen et al. 2013a, Holland 2014) seems to be the only mechanism available to many inexperienced animals that travel without experienced companions (Berthold 1999, Mouritsen 2003, Mouritsen et al. 2013a,b, Holland 2014, Perdeck 1958, Mouritsen and Mouritsen 2000, Deutschlander et al. 2012, Holland and Helm 2013."	**Yes**	Indirect
Muheim, R., Schmaljohann, H. and Alerstam, T. 2018. Feasibility of sun and magnetic compass mechanisms in avian long-distance migration. – Move. Ecol. 6:8	Review	"Young, inexperienced birds on their first migration are generally assumed to use a genetically encoded program, providing them with information on the direction and distance to migrate (Berthold 1990, Gwinner 1996, Gwinner and Wiltschko 1978). Navigational map information collected during this first migration allows them then to navigate back to the known breeding area and during future migrations, as has been shown by several displacement experiments (Perdeck 1958, Thorup et al. 2007, Chernetsov et al. 2008)."	**Yes**	Indirect

Merlin, C. and Liedvogel, M. 2019. The genetics and epigenetics of animal migration and orientation: birds, butterflies and beyond. – J. Exp. Biol. 222	Review	"Genetic inheritance of both timing and migratory direction was further supported by elegant displacement experiments in which both experienced adults that already had successfully completed a migratory journey and naïve juvenile birds on their first journey were displaced from their original location (Perdeck 1958, Thorup et al. 2007). **Inexperienced juveniles followed an innate clock and compass strategy** (e.g. vector navigation), leaving at the right time and flying the correct distance **in the inherited migratory direction**."	**Yes**	Direct
Verhoeven, M.A., Loonstra, A.H.J., Senner, N.R., McBride, A.D., Both, C. and Piersma, T. 2019. Variation from an unknown source: large inter-individual differences in migrating Black-tailed Godwits. – Front. Ecol. Evol. 7:31	Topical	All of these experiments should manipulate the spatiotemporal environment during development, thus enabling an evaluation of whether the environment does or does not affect the migratory behavior of juveniles. If it does not, this would be evidence for innate migratory behavior (Perdeck, 1958, Thorup et al. 2007).	**Yes**	Direct

[1] Strange statement, as other authors have interpreted one-direction orientation as 'vector navigation'!

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